

ORIGINAL ARTICLE

Parental relatedness and parasitoid sex ratios under local mate competition

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Abstract

Sex ratio theory predicts that, under local mate competition, a more female-biased offspring sex ratio will be produced by females when their relatedness to their mates is closer. We assess how the sexual composition of broods responds to mother–mate relatedness using *Goniozus legneri* Gordh (Hymenoptera: Bethyridae), a parasitoid wasp that has biased sex ratios due to local mate competition. Relatedness was varied by providing virgin females with a mate that was either a sibling, a non-sibling from the same strain, from a strain with geographically similar origin or from a strain with geographically distant origin. The sex ratios among broods produced by mothers that had mated with a sibling or a same-strain male were similar and were more biased than broods produced by females mated with males from a different strain. Brood sex variances were higher after mating with different-strain males. Previous evaluations of parasitoid sex ratio responses to mate relatedness have not found the patterns predicted, possibly because the species investigated can control progeny sex ratio but cannot discriminate kin. In contrast, female *G. legneri* appear to possess both these abilities and appears to respond to mate relatedness in qualitative agreement with theoretical predictions.

Key words: brood sex ratio, *Goniozus legneri*, kin discrimination, sex ratio variance.

INTRODUCTION

Evolutionary theory predicts that the optimal sex ratio for a mother to produce should depend on the number of mothers contributing offspring to a future mating group. When there are one or a few mothers (termed foundresses), strong female-bias is selected for as a result of the advantages of reducing competition for local mating opportunities between sons and increasing the number of mates for each son; the theory is known as “local mate competition” (LMC) (Hamilton 1967; Green *et al.* 1982; Herre 1985; Orzack *et al.* 1991; Greeff 1996; West 2009; Chung *et al.* 2019). Extending theory for strict LMC (under which all mating occurs prior to dispersal from natal groups, Hamilton 1967) to consider different degrees of pre-mating dispersal (partial LMC) predicts that non-local mating selects for

less biased sex ratios among broods (Nunney & Luck 1988; Hardy 1994). Under LMC, selection also favors low sex ratio variance, although subsequent developmental mortality could act to increase variance across broods and select for higher brood sex ratios (proportion of offspring that are male) (Green *et al.* 1982; Nagelkerke & Hardy 1994; Hardy *et al.* 1998; Kapranas *et al.* 2011; Khidr *et al.* 2013b; Wilkinson *et al.* 2016; Chung *et al.* 2019).

Inbreeding is an additional predicted influence on the sex ratios of haplodiploids (females develop from fertilized, diploid eggs; males develop from unfertilized, haploid eggs): it increases mother–daughter relatedness more than mother–son relatedness and favors more female-biased sex ratios under multifoundress LMC (Frank 1985; Herre 1985; West 2009; Gardner & Hardy 2020). The predicted sex ratio effect is found in cross-species comparisons of fig wasps (Herre 1985). Females could, in principle, adjust their offspring sex ratios in facultative response to mating with a sibling or a non-sibling male, to the average levels of inbreeding or utilize fixed sex allocation sequences (Greeff 1996; Reece *et al.* 2004; Chung *et al.* 2019).

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Theory considering (for multifoundress cases) how foundresses should respond facultatively to whether or not they have mated with a sibling predicts that sib-mated females should produce a much more female-biased sex ratio than females that mated with non-sibs (Reece *et al.* 2004; Shuker *et al.* 2004). Tests for a facultative response to mate-relatedness using the gregarious parasitoid wasp *Nasonia vitripennis* have found no effects on sex ratios of broods produced by 1–7 foundresses, seemingly because females are unable to assess their relatedness to mating partners (Reece *et al.* 2004; Shuker *et al.* 2004; Burton-Chellew *et al.* 2008).

Here we test for sex ratio effects of mate relatedness using a gregarious parasitoid species in which females have been shown to attune aspects of behavior according to kinship and that has biased sex ratios due to LMC. *Goniozus legneri* Gordh (Hymenoptera: Bethyilidae) is an ectoparasitoid of lepidopteran larvae that has a life cycle that largely complies to the assumptions of LMC theory and its female-biased sex ratios with low variance comply with the predictions of theory (Gordh *et al.* 1983; Hardy *et al.* 1998, 2000; Wilkinson *et al.* 2016). Due to aggressive host and brood guarding by mothers for several days prior to and after oviposition (Bentley *et al.* 2009), broods are normally produced by a single foundress. Aggression is reduced when competitor females are siblings or perceive each other as familiar (Lizé *et al.* 2012), possibly based on the hydrocarbon composition of their integuments (Khidr *et al.* 2013a): adult females thus have some kin discrimination abilities. Clutches normally range from 4 to 18 eggs but broods may be smaller at maturity due to developmental mortality (Khidr *et al.* 2013b). Males are protandrous, typically mating with their sisters as these mature but males also disperse from natal patches, so some non-sibling mating (partial LMC) is likely (Hardy *et al.* 2000), especially as broods often contain female offspring only (chiefly due to male developmental mortality) (Hardy *et al.* 1998; Khidr *et al.* 2013b). We would not expect effects of mate relatedness under single-foundress strict LMC, because models predict that sex ratio optima are maximally biased under any degree of relatedness (Herre 1985; West 2009; Gardner & Hardy 2020). Under partial LMC, single-foundress sex ratio optima are, however, less biased (Nunney & Luck 1988) and (given that partial LMC and multifoundress LMC are both intermediates between the extremes of single-foundress strict LMC and panmixis, Hardy 1994) facultative responses to sibling or non-sibling mating by single foundresses (similar to those predicted under multifoundress LMC) might be expected. Furthermore,

when locally mated females of the congener *Goniozus nephantidis* are subsequently confined together as multiple foundresses, offspring sex ratios are more female biased when all foundresses are sisters compared to when none are sisters (Abdi *et al.* 2020; Gardner & Hardy 2020), illustrating a similar interplay between relatedness and sex ratios in *Goniozus*.

MATERIALS AND METHODS

Four mating relatedness treatments were established using three strains of *G. legneri*. All strains were reared on larvae of the moth *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae) (Lizé *et al.* 2012). Experiments and cultures were kept at 26°C, 60–80% relative humidity and an 18 h light : 6 h dark cycle. All females used in experiments belonged to a strain originally collected from Santiago, Chile, in 2003 (Zaviezo *et al.* 2007), maintained in laboratory culture in Chile and subsequently cultured in our laboratory since 2009; we refer to this strain as “Chile Lab” (CL) (Lizé *et al.* 2012; Khidr *et al.* 2013b, 2014). Males used in experiments were from the CL strain or one of two further strains. The “Chile Field” (CF) strain was field-collected in Santiago in May 2009 and subsequently cultured in our laboratory (Khidr *et al.* 2013b, 2014). The “U” strain was obtained in 2003 from a commercial insectary in the USA, with the original material believed to have been collected from southern Uruguay in 1978 (Gordh 1982; Gordh *et al.* 1983), approximately 1800 km east of Santiago, and subsequently cultured in our laboratory (Lizé *et al.* 2012; Khidr *et al.* 2013b, 2014). Analysis of DNA microsatellite polymorphisms indicates a lack of variation within each of these strains but consistent between-strain differences (Khidr *et al.* 2013b, 2014). The CL and CF strains are estimated to be more closely related to each other than either is to the U strain (Khidr *et al.* 2014). These strains can readily interbreed (see below and Khidr *et al.* 2013b) and produce offspring with very similar patterns of developmental mortality to those observed in naturally produced U strain broods (Gordh *et al.* 1983; Hardy *et al.* 1998; Khidr *et al.* 2013b).

Relatedness between mates was varied experimentally by placing five to six virgin CL females in a vial with one or two males from a given strain and allowing them to mate for 2–3 days. The number of males and females present, and the timescale for mating, were similar to what are thought to be the natural conditions of maturity and predispersal mating in *G. legneri* (Hardy *et al.* 2000). When males were from the CL strain, they were either siblings of the females (from the same developmental brood) or non-siblings (from a

different brood). In terms of closeness of relatedness between mates, the treatments were thus ranked as “CL female plus sibling CL male” > “CL female plus non-sibling CL male” > “CL female plus CF male” > “CL female plus U male”.

Females ($n = 225$) were then individually provided with a host larva of known weight (range, 31–39 mg) in a stoppered glass vial and the resultant broods were allowed to develop to adulthood. The numbers of male and female progeny developing in these single-foundress broods were recorded. Broods containing only males on emergence ($n = 14$) were likely produced by unmated females that cannot control sex allocation and were excluded from further analysis (following Hardy *et al.* 1998; Reece *et al.* 2004; Shuker *et al.* 2004; Shuker *et al.* 2006; Burton-Chellew *et al.* 2008; Khidr *et al.* 2013b; Abdi *et al.* 2020).

Data from the remaining 211 broods (CL sib, $n = 70$; CL non-sib, $n = 66$; CF, $n = 34$; U, $n = 41$) were analyzed using generalized linear models (GenStat version 19; VSN International, Hemel Hempstead, Hertfordshire, UK). Log-linear analyses with quasi-Poisson error distributions and a log-link function were used to explore effects in terms of numbers of males per brood (Crawley 1992; Hardy *et al.* 1998; Khidr *et al.* 2013b) and to evaluate relationships between brood size and host size. Logistic analysis with quasi-binomial errors and a logit link function was used to explore the effect of mate relatedness treatment on secondary sex ratios (proportion of male offspring within broods) (Orzack *et al.* 1991; Crawley 1992; Hardy *et al.* 1998; Shuker *et al.* 2006; Khidr *et al.* 2013b; Abdi *et al.* 2020). When using empirically estimated scaling parameters to adjust the initial assumption of either Poisson or binomial errors (to become quasi-Poisson or quasi-binomial) to fit better to the data, these likelihood-ratio tests generate F statistics (Crawley 1992).

Brood sex ratio variance was estimated using heterogeneity factors (HF) and variance ratios (R), deviation from binomial variance was assessed using Meelis tests, generating U-statistics (Hardy *et al.* 1998; Krackow *et al.* 2002; Kapranas *et al.* 2011; Khidr *et al.* 2013b; Wilkinson *et al.* 2016) and differences between treatments were evaluated using Bartlett's test for homogeneity of variances, generating χ^2 -statistics.

RESULTS

Females produced larger broods on larger hosts ($F_{1,203} = 221.81$, $P < 0.001$, %Dev = 48.31). The brood size response to host size interacted weakly with mate relatedness ($F_{3,203} = 5.36$, $P < 0.001$, %Dev = 3.55) such

that the rate of brood size increase was greatest when females were mated with sibling males. There was no significant difference in the brood size response to host size between females mated with males from either CF or U (aggregation of factor levels including interaction term: $F_{2,205} = 0.31$, $P = 0.732$, %Dev = 0.133) but the responses by CL females mated with sibling or by non-sibling CL males were different from each other ($F_{2,207} = 5.39$, $P = 0.005$, %Dev = 2.28).

The numbers of males per brood increased with brood size ($F_{1,207} = 43.86$, $P < 0.001$, %Dev = 14.23) and were also affected by mate relatedness ($F_{3,209} = 14.25$, $P < 0.001$, %Dev = 13.87) without significant interaction (relatedness \times brood size: $F_{3,206} = 1.72$, $P = 0.165$, %Dev = 1.67); there were more males produced for a given brood size when females had mated with males from a different strain (irrespective of whether this was CF or U: $F_{1,207} = 0.04$, $P = 0.845$, %Dev = 0.012) than when they had mated with same-strain males (irrespective of sibship: $F_{1,208} = 0.49$, $P = 0.483$, %Dev = 0.185) (Fig. 1A).

The mean brood sex ratio across all replicates was 0.1763 (+SE = 0.0098, –SE = 0.0094) with variance that was not significantly different to binomial (HF = 1.29, R = 1.246; Meelis test: U = 1.98, $P > 0.05$). Sex ratios were significantly affected by mate relatedness ($F_{3,207} = 13.96$, $P < 0.001$, %Dev = 16.51) but not by brood size ($F_{1,206} = 1.92$, $P = 0.168$, %Dev = 0.75) or by an interaction between brood size and relatedness ($F_{3,203} = 2.30$, $P = 0.078$, %Dev = 2.72). There was no significant difference in sex ratios produced following mating with CF or U strain males ($F_{1,208} = 0.01$, $P = 0.936$, %Dev = 0.002%) or following mating with sibling or non-sibling CL strain males ($F_{1,209} = 0.09$, $P = 0.759$, %Dev = 0.04). The mean sex ratio of broods produced by females mated with CL strain males was 0.1321 (+SE = 0.0090, –SE = 0.0085) and had significantly less than binomial variance (HF = 0.852, R = 0.692; Meelis test: U = –2.19, $P < 0.05$); the mean sex ratio produced by females mated with males from a different strain was 0.2499 (+SE = 0.0196, –SE = 0.0186) and had significantly greater than binomial variance (HF = 1.49, R = 1.44; Meelis test: U = 2.49, $P < 0.05$). Sex ratio variance was significantly lower among broods produced by females mated with males from the same strain than among broods mated to males from a different strain (Bartlett's test: $\chi^2 = 35.88$, d.f. = 1, $P < 0.001$).

We conclude that females that had mated with males from the same strain produced more female-biased offspring sex ratios than females that mated with males from another strain (Fig. 1B) and that they also produced sex ratios with lower variance.

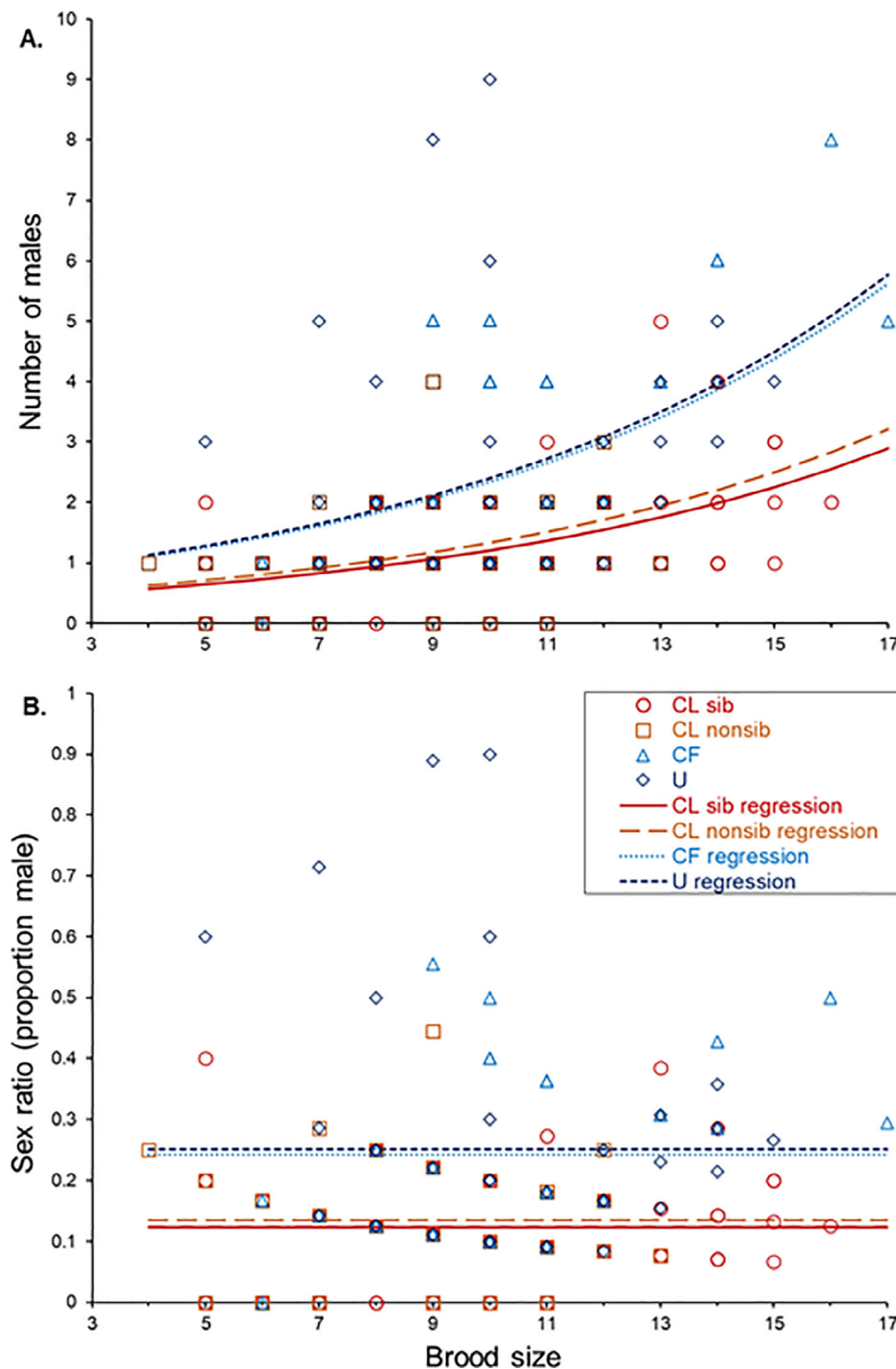


Figure 1 Effect of mate relatedness on brood sexual composition in *Goniozus legneri* Gordh (Hymenoptera: Bethyridae). (A) Number of males per brood produced by females following different mate relatedness treatments. Numbers of males increased with brood size and were also significantly higher when females had mated with a male from another strain (irrespective of strain identity) compared to a same-strain male (irrespective of sibling [sib] status). Separate log-linear regression lines are shown for each mating treatment to illustrate the similarities and differences in responses. The equations for the number of males per brood for all strains have the same slope (0.1251 on the \log_e scale) and are of the form “ $\text{antiLog}_e((0.1251 \times \text{brood size}) + \text{intercept})$ ” with the intercepts for each strain being: “Chile Lab” strain (CL) sib = -1.065 ; CL non-sibling (non-sib) = -0.961 ; “Chile Field” strain (CF) = -0.4 ; “Uruguay” strain (U) = -0.374 . (B) The same data in terms of brood sex ratios. Sex ratios did not differ significantly when mates were either sibling or non-sibling CL males and also did not differ when males belonged to either of the other strains, but were more biased when mates were from the same strain rather than a different strain. Sex ratios did not vary significantly according to brood size: the fitted logistic regression lines thus have no slope and represent the means for each mating treatment. The key is common to both panels.

DISCUSSION

The sexual composition of *G. legneri* broods complied broadly with those observed in prior studies that did not manipulate mate relatedness (Gordh *et al.* 1983; Hardy *et al.* 1998, 2000) and were additionally the most female biased when mothers had mated with closely related

males. Encountering a male from another strain could thus influence a female’s estimation of the probability of inbreeding among her offspring and favor increased investment in males, as predicted under several LMC scenarios (Frank 1985; Herre 1985; Nunney & Luck 1988; Greeff 1996; Reece *et al.* 2004; West 2009; Gardner & Hardy 2020). Less biased sex ratio optima

are, under some scenarios, also expected to reduce selection for low sex ratio variance (West 2009; Wilkinson *et al.* 2016), offering explanation for the higher variances observed among broods produced by females that had mated with males from a different strain. Candidate mechanistic cues for the required kin discrimination are cuticular hydrocarbon profiles, which are known to differ between CL and U strain males (Khidr *et al.* 2013b). However, that similar sex ratios were produced by females mated with sibling or non-sibling males from the same strain suggests females lack the ability to distinguish between relatively close male kin, even though they can distinguish within-strain differences between other females (Lizé *et al.* 2012; see also Abdi *et al.* 2020).

While a straightforward interpretation of our results is that females directly assess their relatedness to the male they mate with and adjust subsequent sex allocation accordingly, there are several further factors that could potentially influence the sex ratio patterns observed. First, developmental mortality can alter brood sexual composition between offspring production and maturity, diminishing maternal influence on secondary sex ratios and increasing sex ratio variance (Green *et al.* 1982; Nagelkerke & Hardy 1994; Hardy *et al.* 1998; Kapranas *et al.* 2011; Khidr *et al.* 2013b; Wilkinson *et al.* 2016). Sex ratios at oviposition were not assessed because such evaluation in *G. legneri* currently necessitates cross-strain mating (Khidr *et al.* 2013b), confounding the purpose of our experiment. Second, strain-specific effects beyond merely “closeness of relatedness” might operate. The weak developmental mortality interaction of female–male strain with brood size observed by Khidr *et al.* (2013b) is compatible with the weak interaction between brood size and mate relatedness we observed. In *N. vitripennis*, strain identity could affect females’ sex ratio responses to LMC cues (Orzack *et al.* 1991), and, in particular, males from different strains might exert differing degrees of influence over a female’s progeny sex ratio, through sexual conflict or genetic incompatibilities (Shuker *et al.* 2006; Geuverink *et al.* 2009). We consider that further work is required to fully separate possible confounds from kin recognition effects in *G. legneri*; it is, however, noteworthy that Khidr *et al.* (2013b) found no primary or secondary sex ratio differences between the offspring of CL females mated with U males and those of U females mated with CL males.

CONCLUSION

Predictions for adaptive sex ratio responses to relatedness assume that mothers are able to both control sex

allocation and discriminate kin. *Goniozus legneri* is known to have both abilities (Lizé *et al.* 2012; Khidr *et al.* 2013b) and we have found that it appears to utilize them in combination to adjust sex ratios as predicted.

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COMPETING INTERESTS

All authors declare that they have no competing interests.

DATA AVAILABILITY

The data generated in the experiments reported in this study are available from the corresponding author on reasonable request.

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